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1 **In Focus. Staying out of the heat: how habitat use is determined by local temperature**

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10 In the marine environment species distributions are closely linked to temperature gradients, but how
11 individual behaviour is affected by local temperatures is less well understood. Frietas *et al.* (2016)
12 tracked Atlantic cod within a Norwegian fjord using electronic acoustic tags. They showed that when
13 surface waters were warm, cod occupied the cold deep non-vegetated habitats. However, when
14 surface waters cooled, fish moved into shallow seagrass and macroalgae beds that were previously
15 out-of-bounds. The study provides a clear example of how thermal regimes determine habitat use
16 over fine spatial and temporal scales, with potential implications for population dynamics under
17 climate warming.

18

19

20 To ensure peak physiological performance animals should occupy an optimal temperature regime.
21 Sub- or supra-optimal temperatures will result in a lower physiological efficiency and be energetically
22 expensive. At extreme critical temperatures, core aerobic physiological processes will fail, ultimately
23 leading to death (Pörtner & Farrell 2008). Due to these major effects that temperature can have on
24 animals it is perhaps not surprising that thermal tolerance is a one of the major drivers of species
25 distributions (Sunday *et al.* 2012). However, life is never simple, and temperature alone does not
26 determine species ranges. Instead species ranges are also determined by the availability of
27 essential resources, such as food and shelter, and the distributions of natural enemies. Thus, the
28 need for optimal thermal habitat can conflict with the need to spend time in other locations (van
29 Beest *et al.* 2012). Animals may benefit when moving from thermally optimal habitats if the costs of

30 staying become too high. Such movement can in principle be determined by how temperature
31 changes over daily, seasonal, or even interannual cycles.

32

33 Atlantic cod is one of the most commercially important species of fish, with recent (2013) estimates
34 of fisheries landings in excess of 1.3 million tonnes per year (FAO 2015). The species has a broad
35 distribution across the boreal waters of the northern Atlantic from northern Europe to Iceland,
36 Greenland and North America (Mieszkowska *et al.* 2009). Many fished populations have historically
37 been decimated by overharvesting, but there are also strong indications that populations have been
38 negatively affected by climatic warming (Brander 2010). Decades of study by fisheries biologists
39 have provided key information on how temperature affects reproduction, growth and longevity in the
40 species (Taylor 1958; Pörtner *et al.* 2001; Kling *et al.* 2007; Righton *et al.* 2010). Moreover, several
41 studies with tagged Atlantic cod have identified temperature as an important factor affecting depth
42 distributions (Neat & Righton 2007; Frietas *et al.* 2015), suggesting an influence of the local
43 temperature regime on individual behaviour. Against this background, it is clear that the species
44 provides useful opportunities to investigate how natural temperature changes affect patterns of
45 habitat use and population demography.

46

47 Freitas *et al.* (2016) tagged individuals within an Atlantic cod population in a Norwegian fjord with
48 acoustic transmitters. Then, using a comprehensive array of receivers they were able to compile
49 information on the location and depth of these fish to the remarkable spatial resolution of less than
50 5m. Uniquely they coupled location data with high quality habitat maps and sea temperature
51 information from underwater data loggers, enabling tests of how habitat use alters with changing
52 temperature. The authors discovered that when temperatures in surface waters were cool ($<16^{\circ}\text{C}$),
53 cod entered the shallows to use eel grass and macroalgae beds where they are presumed to feed.
54 However, when surface waters were warm ($>16^{\circ}\text{C}$), the cod descended into non-vegetated rock and
55 sand habitats characteristic of deeper waters. These results suggest that these fish avoid warmer
56 waters, and only when the surface temperatures cool past a thermal threshold can they use their
57 favoured habitat. It seems that sea surfaces temperatures directly determine the seasonal time
58 window when cod can use shallow water resources.

60 The work of Freitas *et al.* (2016) highlights the link between temperature and habitat use in fish, but
61 the underlying reasons for the correlation can be complex. Warmer waters have lower dissolved
62 oxygen, so rising temperatures can lead to a mismatch between oxygen demand and availability
63 (Pörtner & Knust 2007; Pörtner & Farrell 2008). Thermal shifts may also affect the behaviour and
64 abundance of prey, predator and competitor species of Atlantic cod (Brander *et al.* 2010), perhaps
65 making shallower waters less profitable environments in warmer periods. Due to this complexity a
66 full understanding of how thermal change drives behavioural and abundance changes in populations
67 and communities will be major undertaking, but perhaps the cool-water fjord ecosystem studied by
68 Freitas *et al.* (2016) will be a valuable system in which to undertake such future study.

69

70 Evidence of temperature-dependent habitat selection from Freitas *et al.* (2016) helps to interpret
71 earlier work that shows that Atlantic cod often use thermal habitat that is less than optimal for growth
72 (Neat & Righton 2007). It appears likely that cod are capitalising on resource rich habitats that are
73 thermally tolerable, but less than ideal for growth. Although further work is needed to establish this
74 concept firmly, the results are indicative of fish distributions being dependent upon requirements for
75 both suitable thermal habitat and essential ecological resources. The combination of these needs
76 may be the driver of the spatial patterns of population substructure often seen in cod from both
77 tagging (Neat *et al.* 2014), and genetic studies (Knutsen *et al.* 2011).

78

79 Sea surface temperatures in the North Sea region are projected to rise by 1.8°C over the next 50
80 years (Rutterford *et al.* 2015). Projections of the impacts of such climate change on marine fish
81 distributions to date have been primarily based on bioclimate envelope modelling approaches that
82 extrapolate existing thermal occupancy patterns to projected future environments (Cheung *et al.*
83 2010). By necessity such methods overlook more subtle effects of temperature on populations, such
84 as thermally-driven migrations or shifts in competitive ability (Milazzo *et al.* 2013). It is becoming
85 increasingly clear that population-level responses of marine fishes to climate change may not
86 necessarily always involve active wholesale movement of populations to optimal thermal regimes
87 (Simpson *et al.* 2011; Rutterford *et al.* 2015). Instead we may expect marine climate change to lead

88 to differences in recruitment and survivorship of established local populations that are co-located
89 with the essential resources they need.

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142 **Figure legend**

143

144 Figure 1. Atlantic cod (*Gadus morhua*) and the Tvedestrand fjord Norwegian Skagerrak coast
145 studied by Freitas *et al.* (2016). Photos by Øystein Paulsen (left), and Institute of Marine Research,
146 Norway (right).